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The influence of spatial heterogeneity on the behavior and growth of two herbivorous stream insects

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Abstract Environmental heterogeneity can affect the behavior of organisms, but the consequences of patchiness for organismal energetics (e.g., growth, fitness) are not well understood. This study demonstrates that spatial heterogeneity can affect the growth of aquatic stream insects in laboratory streams, and reveals the behavioral mechanisms for these effects. In a 2×2 factorial design, I experimentally manipulated resource distribution (homogeneous vs. patchy, with the same overall resource levels) and current velocity (fast vs. slow) to investigate the direct and interactive effects of these factors on the drift behavior and growth of two mobile stream grazers, the mayflies *Baetis bicaudatus* and *Epeorus deceptivus*. *B. bicaudatus* nymphs grew larger in environments with homogeneously distributed resources than in patchy environments, and both species grew larger in fast than slow current environments. Patterns of drift behavior over the course of the study corresponded to observed differences in growth. Both species grew to larger body size in treatments where they drifted more successfully among substrates (fast-current treatments) and where they entered the drift less frequently (fast current for both species, and homogeneous treatments for *B. bicaudatus*). Overall, these results demonstrate that patchiness can significantly influence both the behavior of aquatic insects and the size to which these insects grow. In the light of previously published relationships between nymphal mayfly body mass and fecundity, these results suggest that patchiness in streams may have important consequences for mayfly populations.

Key words Mayflies · Spatial heterogeneity · Drift behavior · Growth · Laboratory streams

Introduction

All natural systems are patchy in both space and time. An important goal for ecology is understanding how this heterogeneity affects ecological systems from the level of individual behavior to population dynamics and community organization (Shorrocks and Swingland 1990). The impact of small-scale heterogeneity on individual behavior has received considerable attention (e.g., optimal foraging literature, see Stephens and Krebs 1986), but our understanding of the effects of patchiness at this scale on population-level phenomena is less complete. Recent theoretical investigations into the links between individual behavior and population processes (reviewed in Sibly and Smith 1984) suggest that behavioral responses to environmental heterogeneity may have important consequences for population dynamics. However, few empirical studies have examined the consequences of patchiness for individual behavior and fitness or fitness correlates (Werner et al. 1983; Morse and Fritz 1987; Pierotti and Annett 1987). Direct tests of the way in which heterogeneity affects growth and reproduction through behavior are necessary to establish the ecological consequences of environmental heterogeneity for populations.

Stream herbivores are an excellent model for the study of the ecological consequences of heterogeneity for individual growth and reproduction. Stream environments are often patchy both in terms of physical (e.g., current, light, substrate) and biological characteristics (e.g., algal densities: Jones 1978; Behmer and Hawkins 1986; Feminella et al. 1989; faunal densities: Downes et al. 1993). Further, stream herbivores are generally small, abundant and short-lived, making them amenable to experimental manipulation.

The importance of patchiness to stream herbivores has received considerable attention. For example, previous studies have shown that herbivore density may be affected by spatial and temporal variation in competitor densities (Hemphill 1991) and predator densities (Peckarsky and Dodson 1980; Peckarsky 1985; Power and Matthews 1983; Power et al. 1985). Less is known, how-

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ever, about how stream herbivores are affected by variability in resource densities. Studies addressing this question have examined consumer behavior under different spatial distributions of resources, demonstrating that resource heterogeneity has important effects on herbivore foraging movements. For example, Hart (1981) found that a grazing caddisfly (*Dicosmoecus gilvipes*) decreased movement rates and increased the degree of turning between moves within food patches relative to search movements between food patches. Similar results were reported by Kohler (1984) for the mayfly *Baetis tricaudatus*. These movement patterns are consistent with area-restricted search (Krebs 1978), and result in foragers spending more time in patches of higher quality.

Poff and Ward (1992) expanded on previous studies of foraging in stream insects by demonstrating that the foraging movements of a caddisfly (*Agapetus boulderensis*) were influenced not only by resource distribution but also by local currents. Larvae moved more slowly in high-flow areas, and tended to move either into or lateral to oncoming flow, except in slow current where turning and downstream movements occurred more frequently. Poff and Ward (1992) provided important evidence that the foraging behavior of stream insects can be significantly constrained by heterogeneity in both biotic and abiotic factors.

Clearly, environmental patchiness can strongly influence the behavior of stream insects. However, the extent to which heterogeneity can influence populations is not clear. To address this question, studies must explicitly test the influence of heterogeneity on both the behavior and fitness correlates (e.g., growth, survivorship, fecundity) of animals. This is the major goal of the present study.

Using recirculating stream channels, I investigated the influence of heterogeneity in the spatial distribution of resources and current velocity on the behavior and growth of two herbivorous mayflies (*Baetis bicaudatus* Dodds and *Epeorus deceptivus* Eaton, hereafter referred to as *Baetis* and *Epeorus*) from a western Colorado stream. I created two resource distributions which differed in the distance between resource patches (short distance=homogeneous, long distance=patchy), but had the same overall resource levels. I then superimposed each of two current speeds on these resource distributions. I chose to examine the effects of heterogeneity in resources and current since both are known to affect mayfly behavior (resource distribution: Kohler 1985; Richards and Minshall 1988; current velocity: Minshall and Winger 1968; Corkum et al. 1977; Ploskey and Brown 1980; Ciborowski 1983; Poff et al. 1991). The species used in this study were chosen because they differ in mobility. *Baetis* is a highly mobile swimmer and a dominant component of the drift fauna in the study system, whereas *Epeorus* is primarily a crawler, found much less frequently in the drift (B. L. Peckarsky, personal communication).

Since these species feed only during their nymphal stages, resource acquisition during this time is of critical importance. Adult body mass and egg number are positively correlated for female *Baetis* in the study system

(Peckarsky et al. 1993) and similar relationships have been documented for females from other species (e.g., Brittain 1982). Relationships between adult body mass and male mating success have been documented for *Epeorus longimanus* (Flecker et al. 1988; Allan and Flecker 1989). These data suggest that body mass is a reliable fitness correlate for these mayflies.

The experiment was designed to test two hypotheses. First, I hypothesized that mayflies would drift more and grow less in patchy than in homogeneous environments, since resource patches were separated by greater distances in patchy environments. I also expected that the effects of resource distribution on growth would be stronger for *Epeorus*, whose propensity to drift is lower than that of *Baetis*. Second, I hypothesized that mayflies would enter the drift more and grow less in slow- than in fast-current environments, since preliminary observations indicated that drift movements among substrates were more frequent and less successful in slow flow.

Methods

Study site

Experiments were conducted using mayflies from populations in the East River, a high-elevation stream near the Rocky Mountain Biological Laboratory in western Colorado. All individuals used in this study were collected from a riffle in a second-order stretch of the stream. *Baetis* is bivoltine at this site, and the second generation was used for this study. *Epeorus* is univoltine in this system. Distributions of the two mayfly species overlap both spatially and temporally in the East River, and both graze diatoms from rock surfaces.

Experimental design and conditions

The experiment was conducted over a 9-day period in August 1993. The duration of the study was chosen as a compromise between increasing ability to detect growth differences among mayflies and increasing nymphal mortality with time. I used a complete factorial design with two experimental factors, resource distribution (patchy or homogeneous, hereafter P and H treatments) and current velocity (fast or slow, hereafter F and S treatments). The four treatments were replicated three times and assigned to 12 parallel channels according to a stratified random design. I conducted all experiments in plexiglas circulating stream channels measuring 1.0×0.17×0.1 m (Fig. 1). Using a 0.5-hp irrigation pump, water was drawn directly from the East River, Gunnison County, Colorado, through a 210-μm prefilter, and pumped through 3.8-cm-diameter PVC piping to an open platform adjacent to the stream. Flow was then directed into a series of adjustable gang valves that regulated flow into four water jets in each channel. Water drained from channels at a constant depth of 7.5 cm through two drain pipes in each channel (Fig. 1). Drainage ports were covered with 400-μm Nitex mesh to prevent emigration of nymphs from the channels.

Resource tiles

Unglazed ceramic tiles measuring 15.0×7.6×1.2 cm were used as substrate for mayflies and their periphyton resources. Since mayflies use both the surfaces and undersides of stones in the East River (personal observations), I used ridged tiles which allowed mayflies access to tile undersides during the experiment. To create periphyton resources for mayflies, I placed tiles on floating rafts in

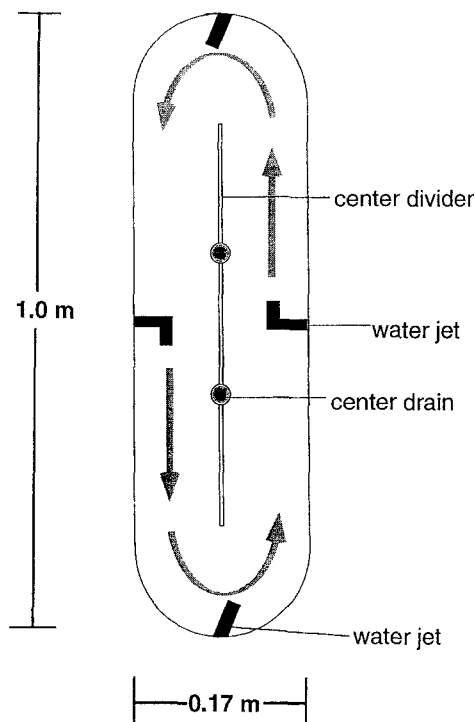


Fig. 1 Diagram of plexiglas recirculating channels. Gray arrows indicate direction of flow. Chamber height=0.1 m

a pool adjacent to the experimental platform. Water flow over the tiles at this site was uniform and approximately 20 cm/s, and tiles were kept at a constant depth of approximately 5 cm. After 11 days of diatom colonization and growth, I removed tiles from the rafts and placed eight tiles in each experimental channel. Tiles were removed from the floating rafts after 11 days since algal communities left ungrazed for more than 2 weeks in the East River become dominated by filamentous green algal species (e.g., *Ulothrix* spp.) normally present in the stream only at very low densities (T.M. Palmer, unpublished work).

To assess starting densities of diatoms, I randomly sampled a 1-cm² area on 15 tiles not used in the experiment with a brush-syringe sampler (Mayer and Likens 1987). Diatom samples were stained with Lugol's iodine and filtered through 0.45- μ m Metrical filters. After allowing the filters to dry, I cleared them with immersion oil and counted diatoms at $\times 1000$. For all algal samples, densities were determined by counting the number of fields required to observe 200 diatoms on linear transects. Using the area of the field, the area of the filter, and the area of substrate sampled, these data were converted to cell density/cm² substrate.

Manipulation of resource distributions

Tiles were placed into experimental channels 1 day before the start of the experiment. To avoid confounding effects of resource distribution with resource abundance on mayflies, I created two resource environments with different spatial distributions of resources but similar overall resource levels (Fig. 2). Eight tiles were placed in H and eight in P treatment channels. H treatments received eight diatom-covered tiles, and each tile was separated from other tiles by 4 cm on both upstream and downstream sides. I denuded tiles in H treatments of approximately 50% of their diatom biomass by scraping 50% of the tile surface with a hard rubber tool in a grid pattern. As a result, diatom patches were present on all tiles in H treatments, and patches (approximately 0.7 \times 0.7 cm) were separated on average by a distance of 0.3 cm, a small distance relative to the scale of mayfly movement (personal

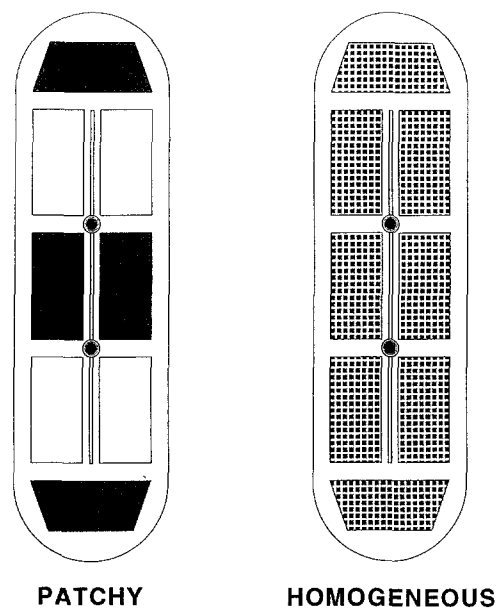


Fig. 2 Diagram of experimental chambers showing arrangement of resources on ceramic tiles (large rectangles). Darkened areas represent unscraped areas colonized by periphyton, and white areas represent scraped areas devoid of periphyton

observations). P treatments received four unscraped diatom-covered tiles and four bare tiles (Fig. 2). Thus, diatom patches were present on every other tile in P treatments, so that mayflies on bare tiles would have to move among tiles to feed. Resource patches in P treatments were separated from one another by approximately 23 cm, roughly 70 times the interpatch distance in H treatments.

To determine the efficacy of the scraping technique used for H treatment tiles, I sampled ten tiles before and after scraping; diatom abundances in the samples were determined as described in the section above (Resource tiles). The scraping technique was effective in removing 94%-98% of all algal cells. Cells remaining at very low densities after scraping were generally adnate forms such as *Cocconeis* and *Achnanthes*. To prevent diatoms from accumulating on scraped surfaces in H treatments and bare surfaces in P treatments, I rescraped these surfaces once daily. To minimize disturbance to mayflies, tiles were scraped only during daylight hours when no or very few nymphs were present on tile surfaces.

At the end of the 5th day of the experiment, tiles were removed from experimental channels and replaced with new tiles colonized in the same manner as the first set. Resource distributions were manipulated and diatom densities were determined on new tiles as described above.

Assessing post-grazing diatom densities and community composition

To determine whether diatom densities differed among treatments after grazing, I randomly sampled 15 grazed tiles from each treatment removed on day 5 and at the end of the experiment. Only diatom-colonized (i. e., non-scraped) areas were sampled; I assumed scraped areas had negligible diatom densities. For P tiles, a single sample from a 1-cm² area was taken. Since H tiles consisted of patches smaller than 1 cm², I combined samples from two adjacent 0.7-cm² patches (total area sampled=0.98 cm²). Diatom densities were assessed as described above.

To establish whether the different flow regimes affected diatom community composition over the course of the experiment, I randomly selected ten diatom samples (used in the above density estimates) from F and S treatments on both day 5 and the end of the experiment and scored them for generic composition. The ge-

neric composition of the first 200 cells encountered on linear transects was recorded, and genera were ranked in terms of abundance.

Manipulation of current velocity

I created two different current regimes in chambers by manipulating flow through each of four gang valves per chamber. During preliminary observations I found that mayfly drift frequency differed markedly between flows equal to or less than 10 cm/s and flows greater than 25 cm/s, so I equilibrated current in F treatments at an average velocity of 35 cm/s (± 8.35 cm/s), and current in S treatments at 8 cm/s (± 3.52 cm/s). Current velocities in both F and S treatments were measured at 12 equidistant points spanning the entire length of the channel. Measurements were taken 1.25 cm above tiles in the center of the channel using a Nixon Streamflo 422 micropropellor current meter. To assess whether oxygen levels differed among the different current treatments, I measured dissolved oxygen (DO) levels with a YSI model 51B oxygen probe.

Realism of treatment levels

Spatial patterns of periphyton communities in the East River and other streams are not well known. My goal in using the H and P resource distributions was to test whether mayflies respond to strong differences in the spatial distribution of algae at small spatial scales. Diatom densities on unscraped algal patches corresponded to intermediate-high density communities in the East River, while scraped tiles had low diatom densities similar to freshly overturned rocks (T.M. Palmer, unpublished work). To assess whether diatom communities on tiles were similar to those on rocks in the East River, I compared the generic composition of five 1-cm² samples taken from granite stones in the stream with five 1-cm² samples taken from experimental tiles. Each sample was processed as described above for diatom density estimates. I then recorded the generic composition of the first 200 cells encountered on linear transects for each sample. I calculated a community similarity coefficient for each of the five sample pairs using the simplified Morisita index (Horn 1966).

Water velocities used in this experiment were within the range of current speeds found in the East River. Benthic samples from the East River indicated that *Baetis* and *Epeorus* are found in both current environments used in this experiment, although densities of both species are roughly 50% higher in the faster flow (T.M. Palmer, unpublished work).

Growth measurements

Baetis and *Epeorus* nymphs were collected from a riffle adjacent to the experimental platform and placed in a storage tank without food for 5 h before the start of the experiment. Nymphs used in the experiment were roughly equivalent in size within each species and corresponded to early stage III (wingpads slightly longer than wide) in the classification of Clifford (1970). To estimate starting weights for the experiment, I randomly chose 35 nymphs of each species from the storage tank and dried them in a drying oven at 60°C for 48 h. I then weighed the nymphs on a Cahn microbalance to the nearest microgram. At the onset of the experiment, 35 nymphs of each species were added to each chamber, corresponding to a density of 377 individuals/m² substrate for each species. Mayfly densities in the East River range between 150–1200 nymphs/m² for *Baetis*, and 50–1000 nymphs/m² for *Epeorus* (Peckarsky 1991). The densities used in this study were relatively low to minimize behavioral interference among individuals and the potential for resource limitation.

At the end of 9 days, I removed all nymphs from the experimental chambers and dried them at 60°C for 48 h. After drying, I weighed nymphs on a Cahn microbalance to the nearest microgram.

Behavioral observations

I began behavioral observations on day 3 of the experiment after allowing the nymphs to habituate to chambers for 2 days. I conducted behavioral trials both during the day (between 0900 and 1600 hours) and at night (between 2130 and 0200 hours). Preliminary observations of chambers indicated that most of the visible activity of these mayflies occurred during the night, so I conducted a broader range of behavioral observations during those hours.

During the night I conducted four types of behavioral observations on nymphs in the four experimental treatments, recording (1) the number of nymphs drifting during 5-min periods, (2) the spatial distribution of nymphs on tiles, (3) the number of drift attempts resulting in successful movement among tiles in fast and slow flow, and (4) the number of drift movements that appeared to result from inter- or intra-specific contact. All nighttime observations were conducted using a dim flashlight fitted with a red filter. Although red light influences the behavior of some mayfly species (Heise 1992), it does not appear to affect the behavior of *B. bicaudatus* or *E. deceptivus* from the East River (personal observations; B.L. Peckarsky, unpublished work).

To quantify drift behavior, I recorded the number and species identity of nymphs drifting either onto, off, or past two adjacent food tiles in the H treatment, or one food tile and the adjacent bare tile in the P treatment, over 5 min. For every drift observation, adjacent tile pairs were chosen randomly to minimize the possibility that unequal numbers of nymphs would be observed among treatments. Only one channel was observed during each 5-min observation period. When nymphs left an observation tile, I kept track of where they settled in chambers, so individuals drifting distances greater than the total length of the chamber were not counted more than once. Accurate observations of drift were possible in fast flow because of the low frequency of drift in these chambers. While drift rates were high in slow flow, simultaneous observations were possible because most drift movements occurred over short distances (i. e., <10 cm) within tiles and immigration rates to the two observation tiles were low. All departures from observation tiles were counted as drift events, including those in which inter-tile movement did not occur.

To compare drift activity in chambers with drift activity in the East River, I calculated drift densities of mayflies in the water column. Drift density was used as an index of drift activity for two reasons. First, the alternative calculation of the proportion of observed larvae drifting per time was not possible, since I made no distinctions during drift observations between (1) individuals drifting off of observation tiles, (2) individuals drifting between observation tiles, (3) individuals drifting onto observation tiles from non-observation tiles, and (4) individuals drifting past observation tiles from non-observation tiles. Second, the only drift data available for the East River are calculated as drift densities.

Assuming that individuals in all drift observations passed a single point in the observation area, I calculated drift densities (the number of nymphs in the water column per m³) for both species using the equation:

$$DD = N_s \times T_m$$

where N_s = the average number of drift events per second (average number of drift observations in 5-min periods divided by 300 s) and T_m = the number of seconds required for 1 m³ of water to pass a point in the channel. T_m was calculated by multiplying the cross-sectional area of the channel (0.0067 m²) by current velocity (0.08 or 0.35 m/s), and dividing that value into 1 m³.

To assess the relative ability of *Baetis* and *Epeorus* to aggregate on diatom covered versus bare tiles in patchy environments, I recorded the position of visible nymphs in P treatments during scans conducted at approximately 2230 hours. On the 3rd night of observations I recorded the number of successful inter-tile drift movements out of 100 drift attempts for both species in fast and slow currents. For these observations, only individuals drifting from the downstream end of tiles were used. Since these nymphs were positioned at the extreme downstream end of tiles, I assumed that nymphs were attempting to drift among resource patches rather

er than within patches, and successful inter-tile drift was defined as drift in which nymphs drifted off of any tile and landed on any tile effectively downstream from their departure point. During nighttime observations, I recorded all instances where drift entry occurred following contact between nymphs.

During the daytime, when fewer nymphs were visible on substrates, I recorded only the number of individuals drifting during 5-min periods. I discontinued daytime drift scans after 3 days since by then almost no drifting individuals had been observed during the day. I visually scanned chambers daily and recorded any mortality.

Statistical methods

All statistical analyses were performed using Systat 5.3 (Wilkinson 1993). Drift data were square-root transformed, and growth data were log-transformed to stabilize residuals. For all analysis of variance (ANOVA) tests, treatment factors (current speed and resource distribution) were treated as fixed effects (Underwood 1981) since their levels were determined by preliminary observations. Drift data were analyzed using two-factor repeated-measures ANOVA. Growth data were analyzed using a two-factor ANOVA. Comparisons of the number of nymphs on food versus bare tiles in patchy environments were made using paired *t*-tests.

Results

Physical characteristics in chambers

Dissolved oxygen levels were close to saturation in all chambers (7.4–7.5 mg/l). Temperature fluctuated daily between 11°C and 14°C and was equal among treatments. Mortality in all chambers was roughly equal (14%–19% for both species); no patterns in mortality were evident among treatments.

Resource tiles

Diatom communities on tiles were similar to those on granite stones in the East River at the generic level; values for the simplified Morisita index of community overlap ranged between 89 and 93% ($n=5$). Diatom densities on tiles introduced at the start of the experiment compared with tiles introduced at 5 days did not differ significantly (*t*-test, $t=-0.674$, 28 *df*, $P>0.5$). Diatom densities on unscraped tile surfaces at the time of introduction averaged 5.64×10^4 cells/cm². Since 50% of the total tile surface in each chamber was scraped, overall diatom density in chambers was 2.82×10^4 cells/cm² (50% of unscraped densities). Variation in algal densities within and among unscraped tile surfaces was low ($SE=2.10 \times 10^3$ cells/cm², approximately 3.7% of the mean).

Current did not affect the rank abundance of diatom genera over the course of the experiment; in both F and S treatments on day 5 and the end of the experiment, the six most abundant genera were ranked *Achnanthes*>*Hantzschia*>*Gomphonema*>*Cymbella*>*Synedra*>*Navicula*.

Average diatom densities after grazing were lower in treatments in which total mayfly growth was higher (Fig. 3). Average post-grazing diatom densities were

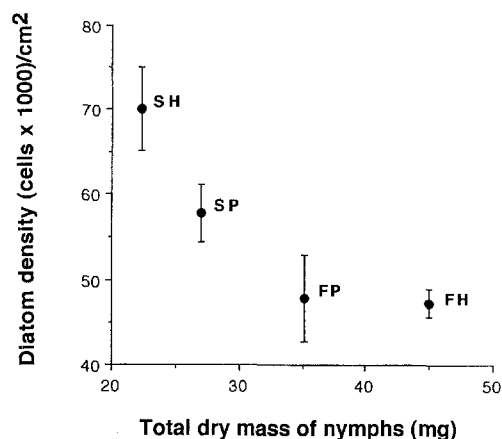


Fig. 3 The relationship between average total nymphal biomass per chamber and average post-grazing diatom densities for four treatments. Letters next to each data point represent treatment type (F fast current, S slow current, H homogeneous resources, P patchy resources). Total nymphal dry biomass was calculated by summing the total dry biomass of all mayflies in each treatment and dividing by the number of replicates per treatment. Average post-grazing diatom densities for treatments were calculated by averaging pooled samples from non-scraped areas taken from day 5 and day 9 of the experiment. Error bars are ± 1 SE of diatom densities

lower than average starting diatom densities in F treatments, and higher than average starting diatom densities in S treatments.

Mayfly body mass

Mayfly growth over the 9-day experiment varied among treatments (Fig. 4). For *Baetis*, both current speed and resource distribution had a significant effect on final nymphal body mass ($F_{1,8}=15.73$, $P<0.005$, $F_{1,8}=6.82$, $P<0.05$, respectively). Nymphs grew larger in fast current, and in H than in P environments within a given current speed (Fig. 4a). There was no significant interaction between current and resource ($P>0.1$). Growth of *Epeorus* nymphs was greater in fast current ($F_{1,8}=11.89$, $P<0.01$) but was not influenced by resource distribution ($P>0.5$) (Fig. 4b). There was no significant interaction between current and resource ($P>0.45$). *Epeorus* nymphs in S treatments lost weight over the course of the experiment.

Drift observations

Current speed affected the ability of nymphs to move successfully among tiles in drift attempts. In F treatments, both mayfly species moved successfully among tiles in 100% of all drift attempts ($n=100$ for both species). In drift attempts in S treatments, the success rate for *Baetis* was reduced to 24%, while the success rate for *Epeorus* dropped to 12% ($N=100$ for both species).

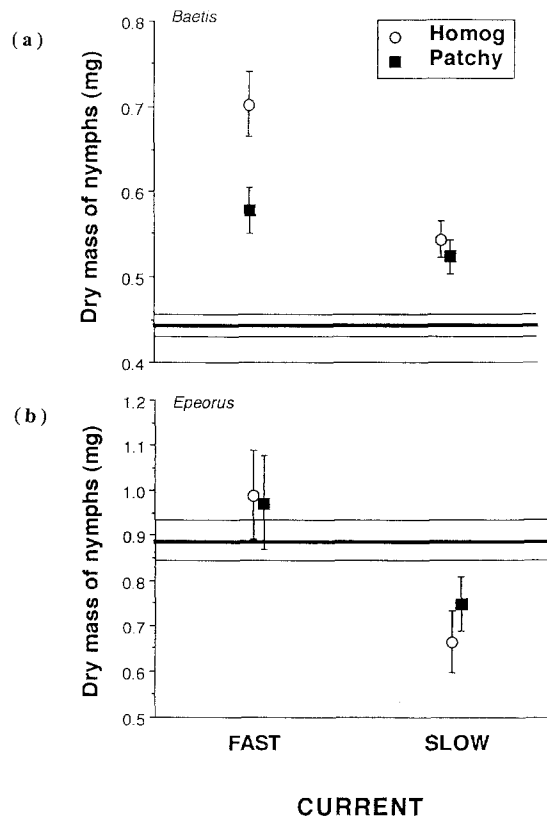


Fig. 4 Mean final dry mass ± 1 SE of **a** *Baetis bicaudatis* and **b** *Epeorus deceptivus* nymphs from four treatments. For both figures, horizontal bar represents mean ± 1 SE initial dry mass of nymphs of each species used in the experiment (open circles homogeneous resource distribution, closed squares patchy resource distribution)

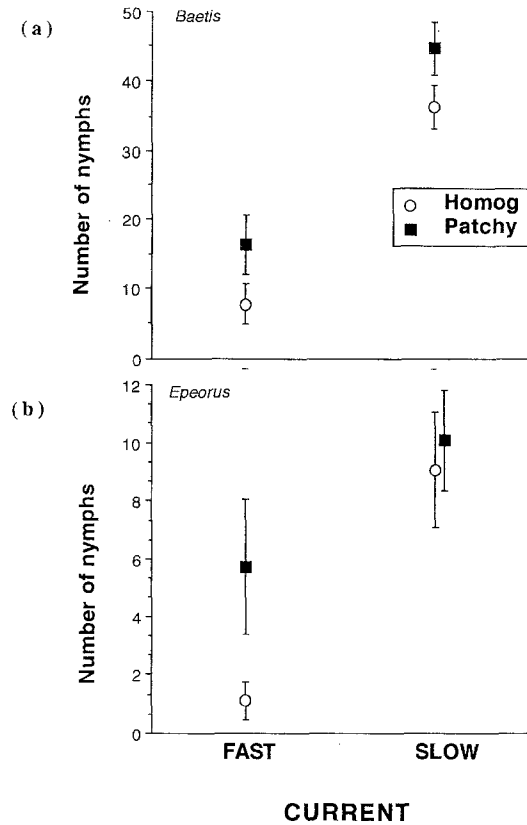


Fig. 5 The mean number of **a** *B. bicaudatis* and **b** *E. deceptivus* nymphs observed drifting during 5-min periods at night in four treatments. Error bars are ± 1 SE. Means and errors shown are from drift data pooled from 6 observation days ($n=18$ observations per treatment) (open circles homogeneous resource distribution, closed squares patchy resource distribution)

During a total of 2.5 h of daytime observations over 3 days I recorded only four instances of nymphal drift; daytime drift observations were therefore discontinued. At night, drift initiation by *Baetis* was significantly higher in S than F treatments (Fig. 5a, repeated measures ANOVA, $F_{1,8}=71.07$, $P<0.001$), and in P than in H treatments ($F_{1,8}=7.07$, $P<0.03$). Nighttime drift frequency of *Epeorus* was significantly higher in S than F treatments (Fig. 5b, repeated measures ANOVA, $F_{1,8}=9.72$, $P<0.02$), but was not affected by resource distribution ($P>0.17$). There was no significant current \times resource interaction with drift for either species ($P>0.3$; $P>0.36$ for *Baetis* and *Epeorus* respectively). The overall magnitude of *Baetis* drift was generally 3–5 times greater than that of *Epeorus*.

Drift densities for *Baetis* were 10.6, 22.8, 218.0 and 280.0 individuals/ m^3 in FH, FP, SH and SP treatments respectively. Values for *Epeorus* were 0.70, 4.21, 1.44 and 1.60 individuals/ m^3 for FH, FP, SH and SP treatments respectively.

Spatial distributions

In P treatments, *Baetis* aggregated more on diatom covered tiles than *Epeorus* at both current speeds (Fig. 6).

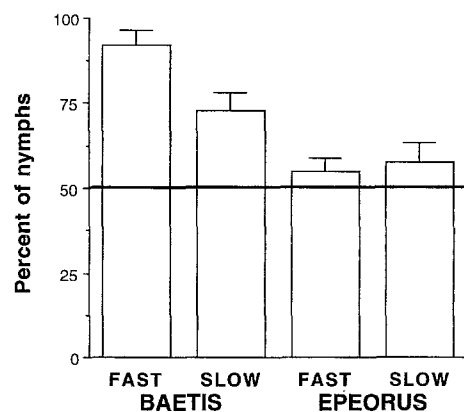


Fig. 6 The mean percentage of *B. bicaudatis* and *E. deceptivus* nymphs observed on diatom-covered tiles (expressed as percentage of total observations on both diatom covered and bare tiles) in patchy treatments in fast and slow flow. Error bars are ± 1 SE. Horizontal bar indicates a hypothetical even distribution of nymphs on diatom-covered and bare tiles ($n=3$ observations per treatment)

Densities of *Baetis* were significantly higher on diatom covered than bare tiles at both current velocities (paired *t*-tests, $t=4.94$, 2 *df*, $P<0.04$; $t=7.12$, 2 *df*, $P<0.02$ for fast and slow current, respectively), whereas densities of *Epeorus* nymphs on diatom covered and bare tiles did not differ significantly in either current velocity ($t=1.80$, 2 *df*, $P>0.2$; $t=0.90$, 2 *df*, $P>0.4$ for fast and slow current, respectively). On average I observed approximately 50% of all *Baetis* nymphs and 43% of all *Epeorus* nymphs on tile sides and surfaces during these scans.

Discussion

Results from this study are consistent with studies documenting behavioral responses of stream insects to abiotic and biotic heterogeneity (reviewed in Wiley and Kohler 1984). Further, this study provides evidence that environmental heterogeneity can affect mayfly growth. Because body size is an important fitness correlate for mayfly females in this system (Peckarsky et al. 1993), these results indicate that heterogeneity in resource distributions and current velocity may have important consequences for mayfly fitness. The relationship between heterogeneity and the growth and fitness of organisms has seldom been examined in any system (Morse and Fritz 1987; Werner et al. 1983); to my knowledge this study is the first to test the effects of spatial variability in resources on the behavior and growth of stream consumers.

Comparison of drift behavior with field data

In this study, heterogeneity in resources and current affected mayfly drift. Drift densities of *Baetis* in fast current were within the range but at the high end of summer drift densities for *Baetis* in the East River (2–25 individuals/m³, B. Kerans, unpublished work), while drift densities of *Baetis* in slow flow were markedly higher than the highest published values for this genus in natural systems (e.g., 60/m³, Clifford 1972). Drift densities of *E. deceptivus* in the East River are not known, but the values reported in this study are considerably higher than peak drift density estimates reported for *Epeorus longimanus* from the Dolores River in Colorado (0.012/m³, Stewart and Szczytko 1983).

Several factors likely contributed to the relatively high rates of drift observed in this experiment as compared to field data. First, the drift density calculation used in this study is a function of water discharge. Although the density of mayflies per unit area of substrate used in this study was within the range of densities in the East River, there is a greater ratio of water volume: substrate area in the East River. Thus, for an equivalent proportion of the total benthic density of mayflies drifting in the water column in the East River compared with experimental chambers, drift densities in the East River will be lower since there is a greater volume of water moving over the substrate per unit time. Since channels used in

this experiment were only 7.5 cm deep, drift densities were likely inflated as a result.

Second, average current velocities for both F and S treatments were estimated from measurements taken in the center of the channels, but flow appeared to be slower in other areas (e.g., sides of the channel, inside the bend at channel ends). In S treatments, this resulted in small areas where current was negligible. Nymphs drifting in these areas were displaced only very short distances (<2 cm), and usually continued to enter the drift repeatedly until they were displaced into the faster-flowing central area of the channel (personal observations). Since each departure from tiles was counted as drift irrespective of the distance moved, these repeated drift attempts in slow flow contributed to the high drift frequency of nymphs in these treatments.

Third, drift densities in this experiment may have been high relative to field estimates as a result of the high proportion (50%) of substrate with very low algal densities. If mayflies rarely encounter substrates devoid of periphyton in the East River, and they react to such encounters by rapidly entering the drift, then drift estimates in this experiment may in part reflect unnatural resource distributions.

Finally, it is possible that the population of mayflies used in this experiment was not a random subsample of individuals from the East River. To obtain nymphs for this experiment, I disturbed substrates from a variety of locations in a nearby riffle, and collected individuals from the drift using a D-net. If mayflies differ in their propensity to drift, resulting from genetic (Minshall and Peterson 1985) or physiological (e.g., pathogenic or parasitic infection, Wilzbach et al. 1988) predispositions, then it is possible that a larger proportion of individuals with high drift propensities were collected than is representative of mayflies in the East River.

Effects of resource distribution on growth rates

In fast current treatments, where drift densities approximated those in the East River, reduced growth of *Baetis* in patchy relative to homogeneous treatments probably reflects lower foraging efficiency in environments with coarser-scale resource heterogeneity. For example, *Baetis* nymphs spent time, albeit brief, searching for food on bare tiles in patchy environments (personal observations). By contrast, *Baetis* moved quickly between adjacent high- and low-density diatom patches in homogeneous environments, which may have increased average feeding rates for mayflies in H relative to P treatments. Other studies have shown that *Baetis* aggregates in areas of high resource density in the field at both small (e.g., individual stones, Richards and Minshall 1988) and large (e.g. stream reaches, Behmer and Hawkins 1985) scales. Results from this study demonstrate that strong variation in small-scale resource heterogeneity can affect mayfly behavior and fitness within a relatively short time. Further study is needed to establish the consequences of nat-

ural levels of resource heterogeneity at different spatial scales for the growth and fitness of lotic invertebrates.

Effects of current on growth rate

The effects of current speed on mayfly growth were similar for both species; mayflies attained larger body size in fast than in slow current. In fast current, mayflies drifted successfully among substrates in all attempts, which may have increased average feeding rates relative to slow current treatments in which mayfly drift among tiles was impeded. Further, unnaturally high drift densities in slow current for *Baetis* may have contributed to low growth for this species in S treatments if the time allocated to drifting was sufficient to affect average feeding rates. However, since observations were conducted over a limited portion of the activity cycle of mayflies, this interpretation is equivocal.

While *Baetis* increased in average body mass in all treatments, average mass of *Epeorus* increased only in fast current. The most plausible explanation for poor growth of *Epeorus* in slow current is that movement among tiles was severely restricted. This species primarily crawls, and crawling among tiles appeared to be inhibited by the plexiglas substrate between tiles; both species were rarely observed crawling between tiles. Where this was coupled with their inability to drift efficiently among tiles in slow flow, *Epeorus* nymphs may have been effectively stranded on tiles in these treatments.

Overall, these results demonstrate that current can significantly constrain both the movements of mayfly nymphs among resource patches and mayfly growth. The implications of these findings for field settings are qualified by unnaturally high drift densities in slow-current treatments, in part resulting from high drift in areas of negligible current. However, it should be noted that in natural systems, riffle-dwelling organisms are often found in areas with negligible (i. e., <1 cm/s) current such as pools (Walton 1980) and stream margins (personal observations). Whether displacement of organisms into these habitats represents a significant cost to individuals has not been established.

Mechanisms for the effect of resource distribution on drift behavior

The effect of resource heterogeneity on *Baetis* drift observed in this study is consistent with Kohler (1985) who reported increased drift with increased resource patchiness for *Baetis tricaudatis*. Contrary to the results of Kohler (1985), however, *Baetis* in this study displayed significant drift even in environments where resources were homogeneously distributed. This observation indicates that for *Baetis* some baseline level of drift occurs even in habitats where food is present on all substrates. Individuals may depart substrates when local resource density falls below some critical threshold (Kohler

1985). Alternatively, periodic drift may allow mobile nymphs such as *Baetis* to assess patch quality at scales larger than that of a single rock. In this study, *Baetis* nymphs aggregated on resource substrates in P treatments, apparently as a result of higher emigration from bare substrates and lower emigration from diatom-covered substrates. This result is consistent with Richards and Minshall (1988) who demonstrated that *Baetis* in an Idaho stream aggregated on rocks with higher relative algal abundance. Drift may also function in aggregation with resources at much larger scales. In their work on an experimentally fertilized Alaskan river, Hershey et al. 1993 (see also Hinterleitner-Anderson et al. 1992) demonstrated that *Baetis* density increased through drift in the fertilized section relative to an unenriched upstream control section. Other studies have shown that *Baetis* aggregates in stream reaches with the highest algal production (Behmer and Hawkins 1985; Wallace and Gurtz 1986). Results from these studies suggest that drift may be an important component of the foraging strategies of some stream taxa.

In contrast to *Baetis*, *Epeorus* nymphs did not show a significant drift response to resource distribution. This pattern likely resulted from the lower drift propensity of this species.

Alternative explanations for the effects of resource distribution on drift behavior

Several alternative explanations exist for the effects of resource distribution on mayfly drift behavior. First, higher average grazer densities on resource tiles in patchy environments may have resulted in increased interference and/or decreased algal densities in these treatments. Both interference (Elliott 1967) and low food levels (Hildebrand 1974; Keller 1975; Bohle 1978; Kohler 1985; but see Ciborowski 1983) have been shown to positively affect drift frequency. However, I observed drift resulting from inter- or intra-specific contacts among mayflies only six times in >10 h of observation; four of these observations were in P treatments, once on a non-food tile. These data suggest that interference was not a significant factor influencing drift in this study, consistent with observations that *Baetis* drift is not density dependent (Kohler 1985; Hinterleitner-Anderson et al. 1992). Further, post-grazing algal densities suggest that resource levels were not uniformly lower on food tiles in P than in H treatments, indicating that differential exploitation among P and H treatments is not a probable explanation for observed drift patterns.

Mechanisms for increased drift in slow current

Increased drift entry in S treatments observed in this study is consistent with other studies reporting increases in drift following flow reduction (Minshall and Winger 1968; Corkum 1976; Corkum et al. 1977; Poff et al.

1991). Although the specific causes for increases in drift in slow current are difficult to discern, there are several potential explanations. If it is assumed that nymphal drift simply represents inter-substrate food searching behavior, then higher rates of drift entry would be necessary in slow flow to search for food among tiles, since a much lower proportion of inter-tile drift movements were successful in S treatments. Under this scenario, nymphs should increase rates of drift in slow flow when food is distributed more patchily, which was the case for *Baetis*. *Epeorus* did not show drift responses to patchiness at either current speed in this experiment, suggesting that drift may not be an important part of the foraging strategy of this species.

Alternatively, if slower current speeds are suboptimal in some way for these mayflies, increased drift in slow flow may represent attempts by nymphs to move into areas with faster current. The simplest explanation for mayfly current preferences involves DO levels. Although DO levels were equivalent among treatments and close to saturation at all times during this study, differences in current speed among treatments may have affected the rate of oxygen renewal to the boundary layer surrounding the respiratory surfaces of nymphs (Wiley and Kohler 1984). Through its impact on oxygen availability, current has been shown to affect both activity level and metabolic rates (e.g., Feldmeth 1970) as well as the positioning behavior and mortality of lotic invertebrates (Wiley and Kohler 1980). In this study, none of the behaviors typical of respiratory stress in *Baetis* ("somersaulting" behavior, Hughes 1966, and positioning of abdomen away from substrate, personal observations) or *Epeorus* (abdomen held away from substrate, personal observations) were observed at any time, and mortality rates did not differ among treatments. These results suggest that if oxygen stress was a factor in slow current treatments, it occurred only at low levels. However, since the possibility exists that low-level respiratory stress occurred in slow-current environments and was not detected, the potential contribution of this factor to observed differences in behavior and growth among current environments should not be ruled out.

Another factor that may influence the suitability of different current environments is predation risk. T. M. Palmer (unpublished M.S. thesis, University of Wisconsin, Madison) demonstrated that *Baetis bicaudatus* suffered greater stonefly (*Megarcys signata*) predation in slow than fast flow (10 cm/s and 35 cm/s, respectively), likely resulting from decreased success of this mayfly's swimming escape response and more conspicuous swimming behavior in slow flow. If risk of predation (e.g., probability of encounter, attack or capture) to mayflies is current-dependent, movement among different current regimes via drift may in part function to minimize this risk. Several other studies have shown that predator-prey interactions in streams can be mediated by flow (Peckarsky et al. 1990; Hansen et al. 1991; Hart 1992). The topic warrants greater attention, since current can strongly affect both the distribution (Hynes

1970) and a wide range of behaviors (Statzner et al. 1988) in lotic animals.

Finally, current speed may affect habitat suitability through direct effects on algal communities. For example, current may influence both the abundance and taxonomic composition of algal communities (e.g., Poff et al. 1990) which may in turn affect the suitability of algal patches for grazers. In this study, post-grazing algal samples indicated that the relative abundances of algal genera did not differ greatly between communities in F and S treatments, but treatments did differ in terms of diatom densities. However, nymphs drifted most and grew least in chambers with the *highest* average post-grazing diatom densities. Since low growth and high drift entry were not related to low diatom abundance in chambers, these results indicate that the effects of current on nymphal drift and growth did not result from current-mediated impacts on algal abundance. Rather, post-grazing diatom abundance in chambers appeared to result from differential consumption among treatments.

This study provides evidence that the spatial distribution of resources in a stream environment can influence both the drift frequency and growth of mobile stream herbivores. Further, current speed affected both the drift behavior and growth of two mayfly species. These results suggest that patchiness in streams may have important consequences for lotic animals both at the individual and population level. A better understanding of the links between lotic animal populations and their resources will require more thorough characterization of the spatial and temporal distribution of resources and flows in streams, and the behavioral and fitness responses of consumers to heterogeneity across a number of spatial scales. Future work in this area should provide critical insights into the consequences of spatial and temporal heterogeneity for the dynamics of populations, and the links between individual behavior and population processes.

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